

LXIII.—On the Reproduction of the Tripylean Radiolaria
(*Phæodaria*). By Dr. A. BORGERT*.

DURING my sojourn this year at the Zoological Station at Naples there was afforded to me in the months from January to May the opportunity, vainly sought for in former years, of studying more closely the conditions of reproduction in the Phæodaria. The special subject of my investigations was *Aulacantha scolymantha*. In the case of this form I succeeded in observing direct as well as mitotic nuclear division and in following in detail the processes that take place therein.

In **direct nuclear division** we observe no gradual constriction, but rather a cleavage of the nucleus into two halves of approximately equal size. The cleft, which originally is quite narrow, grows broader in subsequent stages, and the two halves of the nucleus separate one from the other and become rounded off. These changes in the interior of the central capsule are accompanied by others which are external.

Thus we note the appearance of an annular shallow groove with sharply defined edges on the surface of the central capsule. This groove lies in the same plane as the cleft passing through the nucleus, *i. e.* vertically to the frontal plane †, and divides the main aperture. Instead of the single main aperture originally present two such apertures are formed. Between the edges of the groove the capsular membrane is very delicate. It therefore easily happens that in isolating a central capsule in process of division the two halves come apart in the groove. This is also the spot at which in binary fission the severance of the daughter capsules takes place. Each of these individuals has to supply a secondary aperture by new formation, since in the process of fission it receives only one. Certain figures published by R. Hertwig ‡ and Haeckel § undoubtedly refer to the direct mode of division. Similarly it is evident that Karawaiew ||, during his investigations upon *Aulacantha*, frequently ob-

* Translated by E. E. Austen from the 'Zoologischer Anzeiger,' Bd. xix. no. 507 (July 6, 1896), pp. 307-311.

† I follow the example of Haeckel in designating by the term "frontal" plane that in which are situated the three apertures of the central capsule.

‡ R. Hertwig, 'Der Organismus der Radiolarien,' 1879, Taf. ix. fig. 2, Taf. x. fig. 2.

§ E. Haeckel, "Report on the Radiolaria collected by H.M.S. 'Challenger' during the years 1873-1876," 'Challenger' Reports, Zoology, vol. xviii. pl. ci. fig. 2.

|| W. Karawaiew, "Beobachtungen über die Structur und Vermehrung von *Aulacantha scolymantha*, Haeckel," Zool. Anz. Bd. xviii. (1895) pp. 286-289 and 293-301.

served specimens that were engaged in direct division. Nevertheless he appears erroneously to have regarded them as later stages of indirect nuclear division.

The occurrence of **mitotic nuclear division** in *Aulacantha* was first established by Karawaiew, who, however, observed only a portion of the entire series of stages.

In the resting nucleus the arrangement of the chromatin resembles a coarse sponge. When the nucleus is preparing to divide the framework gradually becomes finer and finer, until at last there is formed in the cavity of the nucleus the characteristic ball of thread. The thread is very fine and extraordinarily closely coiled, so that one is unable to say whether the ball consists of a single long thread or of several such threads. At a later stage the ball presents a looser appearance, and at this period a longitudinal cleavage of the chromatin thread takes place. Thus far we have been able to follow Karawaiew's series of pro-phases ("Prophasen").

As a closer investigation teaches us, the thread in the stage last described consists of a number of sections (chromosomes), after the longitudinal cleavage of which a complete separation of the daughter threads is effected. Now, after the disappearance of the nuclear membrane also the segments of the nucleus arrange themselves in the shape of a plate, which passes from the main aperture towards the opposite side, and so divides the contents of the central capsule into two parts. At the same time the plate does not lie in one plane, but is warped, so that in a certain position its edges form a figure in the shape of an 8. Individual differences moreover prevail with respect to the amount of the twisting. At this stage another longitudinal cleavage of the segments takes place, whereby the division of the equatorial plate into the two daughter plates is ushered in. On the completion of this process also the daughter plates move further apart, at the same time becoming transformed into parallel plane disks somewhat smaller in diameter.

Since Karawaiew also observed this stage, but has not described the structure of the plates properly, I must dwell on it for a moment.

According to Karawaiew each plate is formed of "two different substances." "The bulk consists of a relatively feebly stainable substance, which, on the surface of the plates that is turned towards the centre, projects into the endoplasm in the form of numerous finger-shaped outgrowths; the surface directed towards the periphery is smooth. This larger portion of the plates is permeated by numerous transverse threads, which consist of rows of extremely small

globules, and take a deep stain with safranin; these threads consequently exhibit the property of chromatin."

The sections that I have prepared have led me to a different interpretation, according to which the plates consist of numerous segments of unequal length lying very close together. The finger-shaped outgrowths of a relatively feebly stainable substance, which Karawaiew describes, can only be the ends of the chromatin threads which project further.

Moreover, I am unable to confirm the presence of "two cleft-shaped cavities on the outer surface of the daughter plates," which are said to be "separated from the plasma by a thin and somewhat less transparent layer," and to be filled with nuclear fluid. I would add that, by using a suitable method of fixing, at this stage in the non-vacuolate plasma lying between the plates I was able to observe a fine striation running from one side to the other, and, further, that in somewhat more advanced stages the future plane of severance is to be found already indicated halfway between the plates.

I will here pass lightly over the further processes leading to the reconstruction of the daughter nuclei. They consist in the plates becoming bent, each with the concave side towards the other plate, so that each of them assumes the shape of a bowl. Then they gradually become more and more rounded off, until finally even the last small depression disappears. The further changes in the structure of the daughter nuclei, which, as also the mother nucleus, exhibit a fine membrane, represent a retrograde recapitulation of the first pro-phase stages. The arrangement of the chromatin in the shape of a thread, which still remains distinctly visible for some time, especially in the outer layer of the nuclei, at last gives way to the spongy disposition characteristic of the resting condition of the nucleus of *Aulacantha*.

After the daughter plates have already become transformed into cup-shaped structures, we recognize on the exterior of the central capsule the first indications of the constriction which now commences. This is announced by the appearance on the aboral side of a slight groove, which, running vertically to the frontal plane, gradually advances further and further, and finally divides the central capsule into the two daughter capsules. Thus, in opposition to what we find in direct division, binary fission of the main aperture does not set in until a relatively late period.

I would remark, further, that no trace of a nuclear spindle and centrosomes could be discovered.

Besides the nuclear stages already alluded to we find others that fit into none of the developmental series discussed above,

but rather, from a certain point onwards, seem to constitute a series of their own.

At a particular stage the nucleus of *Aulacantha* sometimes exhibits a pronounced cordate shape. The tip is directed towards the oral pole, while the notch is situated opposite to it on the aboral side. At the latter spot there arises an invagination into the interior of the nucleus, which, though at first small, continually increases in size. When the internal cavity has attained somewhat larger dimensions, on rotating the central capsule through 90° on its main axis we observe, besides other changes, before all things, a constriction on the oral side of the nucleus. At a more advanced stage the groove has increased in depth, while we notice that the internal cavity is divided into two parts by a septum extending from the oral towards the aboral side. The septum is not simple, but double, and the groove penetrates between its two walls.

There can be no doubt that it is in this plane that the division of the nucleus is effected. Owing to the cavity in their interior the daughter nuclei, on the separation of the halves, possess a shape similar to that exhibited at a certain stage in their development by the nuclei formed by division of the equatorial plate. The finer structure, too, exhibits many points of agreement, since in both cases the chromatin is disposed in threads.

Sometimes, and that not altogether seldom, stages in nuclear division are observed that present an entirely different appearance. In these cases apparently the object aimed at is not attained. Since they do not admit of being ranged under any precise method, I believe that their origin is to be ascribed to a miscarriage of division.

Karawaiew has already alluded to the fact that the division of the central capsule of an individual is not under all circumstances immediately followed by a distribution of the rest of the component parts of the body among the two daughter individuals, but that through repeated division of the daughter capsules the formation of a kind of colony may result. The greatest number of the central capsules met with under such circumstances amounted to five. I recently found a particularly large specimen with as many as eight central capsules.

It still remains for us to refer briefly to a few other stages. In examining our material we now and again meet with specimens in whose central capsule we fail to find the nucleus. Instead, on the application of staining reagents for nuclei the entire contents of the central capsule take a slight stain. A closer study of prepared sections shows that in such cases the

whole of the chromatin of the nucleus has become distributed in the plasma. I have acquired a continuous series of developmental stages right up to the complete dispersion of the chromatin. Later on one finds the cavity of the skeleton filled with numerous multinucleate globules. It is evident that the process leads to the formation of swarm-spores.

Again, other individuals are sometimes met with in which in place of the nucleus there is found a vesicle with a considerably thickened wall that takes a deep stain with hæmatoxylin or carmine. This wall is clothed on the inside with a coat of protoplasm. The most striking feature in these stages consists, however, in the presence of many larger and smaller globules, which, on being treated with osmium or mixtures containing osmium, become black, and seem to consist essentially of fat. They lie arranged in a hollow cup ("Kugelschale") against the inner wall. In other cases we meet with similar structures outside the nucleus in the endoplasm. Sometimes there are only one or two such vesicles, at other times a larger number, even amounting to as many as twelve or more. On their appearance the nucleus undergoes certain changes—indeed, it may even entirely cease to exist as such; in the endoplasm, too, degenerative phenomena take place.

Since it was no part of my plan, in framing the foregoing remarks, to propound far-reaching conclusions and comparisons, I have confined myself to putting together in simple form the most essential observations. In so doing I have touched very briefly even upon the most important points. My detailed paper, which will appear shortly, contains all further particulars.

BIBLIOGRAPHICAL NOTICE.

The Collector's Manual of British Land and Freshwater Shells. By LIONEL ERNEST ADAMS, B.A. Second Edition. 8vo. Leeds, 1896.

A NEW edition of this work will probably be welcomed by many collectors of British land and freshwater shells, as it contains instructions with regard to collecting, the means to be employed, the localities to be searched, the methods of preparing specimens for the cabinet, and remarks upon labelling, mounting, and arrangement of collections, which may be useful to them. By the more scientific student, however, the book will be less appreciated, as some portions of the classification adopted are very archaic, and mistakes have crept in, so that a want of thoroughness seems to pervade the